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ORIGINAL PAPER

What are the strengths and limitations of direct and indirect assessment of dispersal? Insights from a long-term field study in a group-living bird species

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Abstract Molecular methods of assessing dispersal have become increasingly powerful and have superseded direct methods of studying dispersal. Although now less popular, direct methods of studying dispersal remain important tools for understanding the evolution of dispersal. Here, we use data from Siberian jays *Perisoreus infaustus*, a group-living bird species, to compare natal dispersal distances and rates using visual mark–recapture, radio-tracking and microsatellite data. Siberian jays have bimodal natal dispersal timing; socially dominant offspring remain with their parents for up to 5 years (delayed dispersers), while they force their subordinate brood mates to leave the parental territory at independence (early dispersers). Early dispersers moved about 9,000 m (visual mark–recapture, radio-tracking) before settling in a group as a non-breeder. In contrast, delayed dispersers moved about 1,250 m (visual mark–recapture only) and mainly moved to a breeding opening. Dispersal distances were greater in managed habitat compared to natural habitat for both early and delayed dispersers. Molecular estimates based on 23 microsatellite loci and geographical locations supported distance estimates from the direct methods. Our study shows that molecular methods are at least 22 times cheaper than direct methods and match estimates of dispersal distance from direct methods. However, molecular estimates do not give insight into the behavioural mechanisms behind dispersal decisions. Thus, to understand the evolution of dispersal, it is important to combine direct and indirect methods, which will give insights into the behavioural processes affecting dispersal decisions, allowing proximate dispersal decisions to be linked to the ultimate consequences thereof.

Keywords Natal dispersal · Neighbourhood size · Philopatry · Biased dispersal · Genetic population structure

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Introduction

Dispersal, the movement of an individual from one place to another, has important consequences for the genetic structure of populations and their persistence (Hanski and Gilpin 1999; Clobert et al. 2001). Successful dispersers settling in a new population may carry novel alleles that counteract the deleterious effects of low genetic variation and inbreeding (Hamilton and May 1977). Dispersal is, therefore, a pivotal factor in key evolutionary processes such as speciation and extinction (Clobert et al. 2001). Moreover, a species' ability to disperse is likely to play a crucial role in its ability to withstand human introduced selection pressures arising from habitat fragmentation and global climate change (Clobert et al. 2001; Kokko and Lopez-Sepulcre 2006).

The two parameters that have captured the focus of dispersal studies are dispersal distance and rate (Clobert et al. 2001). Prior to the era of molecular methods, dispersal distance and rate could only be estimated by re-observing marked individuals. A shortcoming of this method is that individuals in sedentary species are more likely to be re-observed close to the site where they have been marked (i.e. within a study site), and thus, long-distance dispersers often remain undetected (Koenig et al. 1996). Moreover, it remains unclear if

individuals that have not been detected have died or have successfully dispersed outside of the surveyed area. While methodological advances have been suggested to get around these problems (Baker et al. 1995; Cooper et al. 2008; Hirsch et al. 2012), a more unbiased way to study dispersal distance and rate is to use radio-tags (Koenig et al. 1996). The initial limitations of being unable to locate dispersing individuals carrying transmitters have been overcome for larger species using distance tracking through satellite telemetry or mobile phone systems, and small radio-tags have become more and more powerful (Kissling et al. 2013). Nevertheless, these technologies are still expensive, and thus, the low sample size limits the chance of tracking long-distance dispersers (Koenig et al. 1996).

This limitation of detecting long-distance dispersers has been overcome by advances in molecular techniques that have provided a new understanding of dispersal in a wide range of study systems (Clobert et al. 2001; Prugnolle and de Meeus 2002; Broquet and Petit 2009; Stevens et al. 2010). Current molecular methods allow dispersal distance and rate to be accurately estimated (Watts et al. 2007; Stevens et al. 2010; but see, e.g. Bossart and Prowell 1998), and can be used to understand the population structure of a species (Coulon et al. 2008). Molecular methods are relatively fast and inexpensive in comparison with direct assessments of dispersal such as mark–recapture or radio-tracking (see Table 1) and allow dispersers to be identified a posteriori. Nevertheless, despite the methodological progress in assessing dispersal distance and rate, the process itself remains rarely studied (Doerr and Doerr 2005; Hahne et al. 2011; Lenz et al. 2011; Clobert et al. 2012). This is a consequence of the fact that the most commonly used methods of assessing dispersal do not give any information about the decisions made by individuals regarding when to leave (Ekman et al. 2002; Hewett Ragheb and Walters 2011), where and how to move (Roshier et al. 2008) and where and how to settle (Clobert et al. 2001) (Fig. 1 and Table 1). Dispersal distance and rate are the final result of all these decisions, and consequently, one needs to consider the processes before settlement for a comprehensive understanding of the factors affecting the evolution of dispersal.

Here, we use our study system, the Siberian jay (*P. infaustus*), to compare direct and indirect estimates of natal dispersal distance and rate, and highlight the complexity of factors that can affect dispersal as well as the limitations of both methodologies. We follow the definition of Greenwood and Harvey (1982) who defined natal dispersal as the movement of individuals from the site of birth to that of first reproduction or potential reproduction. Siberian jays live in boreal forests throughout Eurasia on year-round territories in groups of two to seven individuals (Ekman et al. 1994). Groups can be multigenerational and can contain up to five non-breeders besides the breeding pair (Ekman et al. 2001; Griesser et al. 2008). Jays have a single brood each year and in successful broods (mean breeding success=0.49; Table 2), one to five offspring fledge (mean±SE=2.84±0.14). About 30 % of fledglings (one to three fledglings per brood, mean± SE=1.36±0.07) delay dispersal and remain on their natal territory for up to 5 years (Ekman et al. 2001; Griesser et al.

Table 1 Different methods used to assess dispersal reveal: assessment of dispersal with radio-tags gives insight into most processes; molecular assessment does not give insight into proximate factors prior to settlement, however, it is much cheaper than direct assessment of dispersal (radio-tags, visual mark–recapture)

Dispersal factor	Radio-tags	Visual mark–recapture	Molecular methods
Dispersal timing	Yes	No	No
Dispersal rate	Yes	Yes	Yes
Dispersal distance	Yes[a]	Yes[a]	Yes
Fate of unsuccessful dispersers	Yes	No	No
Influence of residents on movement decisions	Yes	No	No
Influence of residents on settlement decisions	Yes	No	No
Effective dispersal[b]	Yes[c]	Yes[c]	Yes
Fitness consequences of dispersal strategy	Yes[c]	Yes[c]	Yes[c]
Cost per disperser	620 €[d]	885 €[e]	4.70 €[f]
Work load per disperser	8.4 days	19.5 days	0.125 days[f]

[a] Biased towards short distances (Koenig et al. 1996)

[b] Successful dispersal resulting in gene flow (Broquet and Petit 2009)

[c] If reproductive success of dispersers is followed up after settlement

[d] 120 € tag, in year 2000, we used 20 tags for 10 dispersers (about every second juvenile becomes early disperser), 6 weeks of fieldwork for 2 persons

[e] 6 weeks fieldwork for 2 persons (total 3,800 €) to cover 50 jay territories twice annually, resulted in 24 years data of 103 dispersers. This cost is lower if visual mark–recapture data are product of other fieldwork

[f] Without costs for fieldwork, when including field costs the price for one disperser increases to 28.45 €, and the workload to 0.275 days per disperser

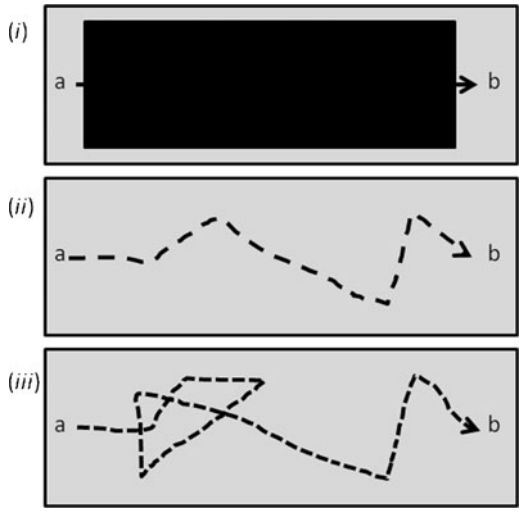

Fig. 1 What do different assessment methods of dispersal tell us? Molecular assessment or mark–recapture methods (MR) (*i*) only give information regarding the dispersal distance and the effective gene flow, but the processes that lead to departure of individuals, during dispersal and settlement remain unknown. Distance tracking (*ii*) gives detailed information of the effective dispersal distance and path, and travelling time (resolution depending on sampling intensity). However, only direct tracking (*iii*) can give detailed insight into proximate factors affecting dispersal: effective dispersal distance, dispersal path and travel time (resolution depending on sampling intensity)

2008). These delayed dispersers aggressively expel their subordinate siblings from the natal territory about 3–6 weeks after fledging (Ekman et al. 2002). Consequently, subordinate siblings disperse and settle as immigrants in other territories (Griesser et al. 2008). Delayed dispersers mainly settle in territories neighbouring their natal territory, possibly to avoid inbreeding (Koenig and Haydock 2004).

First, we examine natal dispersal distance, timing and rate of early dispersers and delayed dispersers using direct methods (visual mark–recapture, radio-tracking) and indirect methods (microsatellite data). So far, studies of dispersal estimates have mainly focused on comparing two of these methods, but not all three. Then, we link these findings with our knowledge on social factors affecting dispersal decisions in Siberian jays (Ekman et al. 2001; Kokko and Ekman 2002; Griesser et al. 2008), to discuss these what natal dispersal distance tells us about dispersal processes in this system. Finally, we discuss this latter question on a more general level to highlight what different methods reveal about dispersal processes and to pinpoint the strengths and weaknesses of the different approaches.

Methods

We studied dispersal in a population of Siberian jays in boreal habitat near Arvidsjaur (65°40′ N, 19°0′ E), northern Sweden. Siberian jays have been studied in this population from 1989 onwards, and the number of monitored territories increased from three to 60 over the study period. The study site consists of two separate areas, one located in heavily managed forest that is dominated by clear-felling (about 30 % of the study site has been clear-felled the last 30 years) and re-plantation of trees. The other area of the study site is located in a forest reserve that has not been affected by forestry at least for 200 years (Fig. 2; Griesser et al. 2007; Griesser and Lagerberg 2012). With the exception of large open areas (clear-felling, young re-plantations, bogs, corresponding to white patches on Fig. 2) or lakes (dark patches on Fig. 2), Siberian jays also occur in most locations outside of our study sites. Thus, our study population is embedded in a more or less continuous population that varies in their density depending on habitat structure (Griesser and Lagerberg 2012).

Almost all birds (with the exception of three individuals that were never caught and ringed) were ringed with unique combinations of one metal and three colour rings for individual recognition at a distance. We routinely collected data on breeding success and group composition in all territories (see Ekman et al. 2001; Eggers et al. 2006; Griesser et al. 2007 for detailed description of methodology). Between 1989–2004 and 2011–2013, we followed the reproduction of most groups in our study population. We caught breeding females before the onset of nesting in March and attached a radio-tag in order to locate the nests and subsequently ring the nestlings. The tag (Holohil BD-2D, Telenax TBX-006) was glued on the two central rectrices and weighed approximately 1.80 g, which corresponds to approximately 2 % of the bird's body mass (80–90 g). The transmitters were shed at the annual moult in June after the breeding season. In years where we did not follow reproduction (2005–2010), groups were visited in spring to monitor group composition and survival of all group members.

In all years of the study, we visited all of the territories in our study population each autumn to colour ring new group members and collect data on dispersal. Unringed members were aged upon capture from the shape of the outermost rectrices, which are more rounded in juveniles (Svensson 2006). Delayed dispersers could be identified because of the continuous ringing of nestlings; any unringed juvenile in a group where nestlings had been ringed, or where we knew that reproduction had failed, was considered to be an immigrant (i.e. early dispersers; $N=186$). On those territories where we lacked information on reproductive success, first-order relatedness of juvenile group members was determined by assessing aggressive interactions between breeders and juveniles on feeders ($N=44$ juveniles years 1989–2004 and 2011–2013; all $N=212$ juveniles years 2005–2010). This method is a reliable indicator of kinship when compared to interactions between individuals of known origin ($N=109$, all correctly classified) (Griesser 2003) or when controlled against DNA fingerprinting $N=13$ (Ekman et al. 1994).

Table 2 Basic population data of the study population showing the yearly total number of territories, the number of territories where breeding was followed, average breeding success, the rate of fledglings becoming early disperser (emigration rate), immigration rate, and population size after immigration in autumn; years 2005-2010 reproduction was not followed

Year	*N* territories	*N* territories reproduction followed	Mean breeding success	Emigration rate	Immigration rate	Population size autumn
1990	13	5	0.60	0.67	0.46	3.56
1991	16	13	0.54	0.45	0.31	2.58
1992	16	14	0.56	0.50	0.19	2.83
1993	15	13	0.38	0.69	0.67	3.22
1994	16	15	0.57	0.73	0.50	3.46
1995	16	11	0.27	0.78	0.13	3.33
1996	15	10	0.10	0	0	2.78
1997	14	13	0.17	0	0	2.36
1998	26	13	0.62	0.72	0.27	2.20
1999	28	23	0.43	0.47	0.46	3.17
2000	38	30	0.50	0.68	0.74	2.96
2001	47	31	0.56	0.69	0.17	2.81
2002	43	41	0.41	0.73	0.81	2.33
2003	41	38	0.51	0.56	0.73	2.88
2004	42	33	0.76	0.82	0.52	3.11
2005	42	0	–	–	0.30	2.81
2006	43	0	–	–	0.49	2.38
2007	44	0	–	–	0.36	2.69
2008	42	0	–	–	0.66	3.17
2009	46	0	–	–	0.52	2.78
2010	50	0	–	–	0.58	2.98
2011	61	49	0.94	0.63	0.34	2.64
2012	57	45	0.45	0.58	0.30	3.26
2013	59	42	0.38	0.72	0.33	2.93
Total/mean	829	439	0.49	0.58	0.41	2.88

Direct assessment of natal dispersal distance

We used two different direct methods to assess dispersal distance: visual mark–recapture and radio-tagging. We analysed data for observations of juveniles that were born on our study site between the years 1988–2004 and 2011–2013 and re-sighted after dispersal either within ($N=63$) or outside ($N=2$) the study sites. We calculated the direct dispersal distance measured between the centre of the territories (Nystrand et al. 2010) and the number of territories that dispersers had travelled through using the average territory size within the study site. We studied dispersal distances with the help of radio-tags in summer 2000 and 2003. In a total of 13 groups, we caught all fledglings before the onset of the dispersal period in June ($N=33$ individuals) and attached radio-tags. After leaving the natal territory, individuals were located daily until settlement, upon which we located dispersers to confirm their settlement in a group (Ekman et al. 2002; Griesser et al. 2008). We radio-tagged $N=46$ delayed dispersers to see whether these individuals had dispersed upon disappearing from the natal territory or had been killed by predators.

To assess the movements of birds outside of the study site, we visited in spring in years 2009 and 2010 and systematically searched the territories adjacent to our study sites (Griesser and Lagerberg 2012), resulting in the recovery of three colour-ringed birds. Given that groups are mobile in autumn, we regularly encountered groups adjacent to our study sites, but within these groups, colour-ringed birds were only rarely re-sighted. However, all of these identified birds were non-breeders that had made subsequent dispersal moves after natal dispersal to acquire a breeding position outside of our study site and thus not included in our analyses.

Direct assessment of dispersal rate

For all years in which we followed reproduction, we calculated the annual dispersal rate of early dispersers that were leaving the natal site (i.e. the proportion of fledglings that became early dispersers), as well as the annual immigration rate of early dispersers.

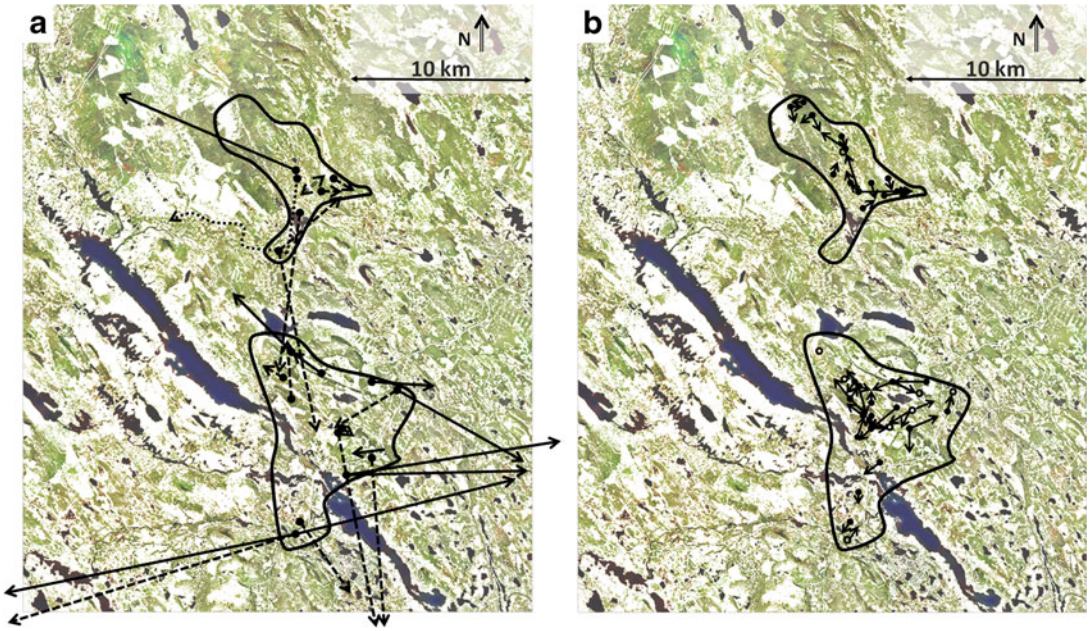

Fig. 2 Aerial image of study sites: northern area (unmanaged habitat); southern area (managed habitat); **a** dispersal movements of early disperser; **b** dispersal movements of delayed dispersers. The natal territories of the disperser are marked with a *filled circle*. In **a**, early dispersers that were followed with radio-tags are indicated with a *solid line*, while early dispersers tracked with visual mark–recapture are indicated with a *dashed line*. One early disperser was tracked continuously after its initial movement southwards (indicated with *dotted line*). Five dispersers moved outside the displayed area (*arrows* extend outside the image). In **b**, delayed dispersers that did not disperse to acquire a breeding opening are indicated with an *open circle*. Aerial image ©Lantmäteriet i2012/921

Statistical analyses

We used generalised linear mixed models in the GLIMMIX module of SAS 9.3 (SAS institute, Cary, NC, USA) to analyse direct dispersal data and assess how dispersal timing affected dispersal distances. We first fitted four commonly used dispersal kernels (Hirsch et al. 2012) and a normal distribution to our all dispersal distances, as well as to those of early dispersers and delayed dispersers separately. Since SAS GLIMMIX does not provide the Weibull function, we choose the most similar function that was available, using the Gamma function instead, and assessed the fit of the different functions using the corrected Akaike Information Criterion (AICC; Akaike 1974). We used both the distribution with the lowest AICC and the one with the least over- or underdispersion (assessed with the Pearson statistics; SAS 2006), and assessed the effect of dispersal timing (early vs. delayed dispersers), the method used to assess dispersal distance (visual mark–recapture, radio-tag) and the study site (managed vs. unmanaged area of study site) on dispersal distance using generalised linear mixed models. Year and territory identity were included as random variables in these models to control for their effect on dispersal distance.

Molecular methods

Blood samples (50–100 μl of blood collected from the alar vein) were taken from all individuals when they were captured for ringing and stored at −70 °C in saline–sodium citrate buffer (Ekman et al. 1994). Genomic DNA was extracted from the blood samples using a high-salt method (Paxton et al. 1996). Sex determination was performed via polymerase chain reaction (PCR) amplification of the CHD gene (chromodomain helicase DNA binding protein) using the primer pairs P2/P8 (Griffiths et al. 1998) and/or 2550F/2718R (Fridolfsson and Ellegren 1999). Sexing using P2/P8 was conducted in 10 μl reactions using 0.25 U Biotaq (Bioline, London, UK), 1× PCR buffer, 0.53 pmol of each primer, 0.13 mM of each dNTP and 2 mM $MgCl_2$. The thermo-cycling profile consisted of 2 min at 94 °C, 30× (30 s at 94 °C, 30 s at 47 °C and 45 s at 72 °C), with a final elongation of 5 min at 72 °C. PCR for 2550F/2718R was conducted in 10 μl reactions with 0.25 U Taq polymerase (Fermentas, St. Leon-Rot, Germany) with 1× NH_4SO_4 reaction buffer, 0.4 pmol of each primer, 0.125 mM of each dNTP and 2 mM $MgCl_2$. The thermo-cycling profile consisted of 3 min at 95 °C, 30× (30 s at 94 °C, 30 s at 51 °C and 1 min at 72 °C), and a final elongation of 7 min at 72 °C. Products were visualised with ethidium bromide on a 1.5–3 % agarose gel or with silver staining on a polyacryleamide gel (Bassam et al. 1991). PCR products were run on a Megabace 1000 automated sequencer s together with ET-400 size standard (GE Healthcare, Pittsburgh, PA, USA) to assess fragment length. Since females are the heterogametic sex in birds, two bands of different size indicate that the sample corresponds to a female and one band indicates it is a male.

Twenty-four microsatellite markers (Jaari et al. 2008) were tagged with a fluorescent dye and divided into three multiplexes (Supplementary Table 1). A PCR was conducted for each multiplex mix using Qiagen Multiplex mix (Qiagen, Hilden, Germany), following the manufacturer's recommendations for PCR with an annealing temperature of 56 °C and 2 μM of each primer. PCR products were diluted 1:100 and electrophoresed on a Megabace 1000 with ET-Rox 400 size standard. Genotypes were scored using Fragment profiler v1.4 software (GE Healthcare).

Genetic assessment of dispersal distance

The genotypes were tested for occurrence of null alleles, large allele dropout and possible scoring errors due to stuttering using Microchecker software (van Oosterhout et al. 2004). Tests for linkage disequilibrium, F_{ST}, effective number of migrants and Hardy–Weinberg equilibrium were performed using Genepop on the web (http://genepop.curtin.edu.au/) (Raymond and Rousset 1995; Rousset 2008). Number of effective migrants was also estimated from $2N_e m_e \approx \frac{1}{4}\left(\frac{1}{F_{ST}}-1\right)$ (Wright 1931, 1943, 1951). The expected heterozygosity (H_e) and number of alleles was calculated with the software SPAGeDi version 1.4c (Hardy and Vekemans 2002).

The spatial structure was tested for all individuals pooled together (N=374), and for delayed (N=151 and early dispersers (N=223) as separate groups using the software SPAGeDi (Table 3). We used two different estimators of pairwise genetic distance: kinship (Loiselle et al. 1995) and Rousset's a (Rousset 2000). Pairwise coefficients like these are typically associated with large standard errors (Vekemans and Hardy 2004), and so to reduce them, we followed recommendations in the SPAGeDi 1.4 user manual (Hardy and Vekemans 2013). We therefore chose distance classes so that the number of pairs within each distance class in the total data set was at least 100, and the proportion of all individuals represented at least once in each interval was at least 0.84. However, due to low sample size (see above), it was not possible to meet these criteria for all distance classes in all of the separate analyses.

We assessed genetic dispersal distance using the slope of kinship estimates against the logarithm of distance, which allows an indirect estimate of gene dispersal distance to be calculated (Rousset 2000; Hardy and Vekemans 2002). This assessment requires an estimate for neighbourhood size $NS = 4\pi De\sigma^2$ (see Wright 1969), which can be calculated from a kinship coefficient ($NS = -(1-F)/\text{blog}_k$) or from Rousset's a ($NS = 1/\text{blog}_a$). We used SPAGeDi to obtain estimates for blog_a (correlation between kinship and log geographic distance), and blog_k (correlation between genetic distance and log geographic distance). Tests for significance were done by bootstrapping with 10,000 permutations. From SPAGeDi, we also obtained jackknifed estimates of mean and standard error for blog.

Dispersal distance was estimated by calculating σ with help of the equation for neighbourhood size (NS) using estimates of NS and the effective population density (see below).

Table 3 Dispersal distances from observational and molecular data and estimated number of territories that dispersers passed through before settling; early dispersers dispersed further than delayed offspring, and radio-tagged dispersers moved further than untagged dispersers that were recovered within the study site

Individual category	N		Dispersal distance (metres±SE)		Number territories passed through (±SE)[a]		Neighbourhood size
Assessment	Direct	Indirect	Direct	Indirect	Direct	Indirect	Indirect
Radio-tagged early dispersers	12	–	8,917±1,535 m	–	7.1±1.1	–	
Untagged early dispersers	15	–	9,000±4,670 m	–	7.2±3.9	–	
Early dispersers (tag and v-m-r)	27	223	8,962±2,627 m	4,250±8,452m[b]	7.0±2.2	3.6±7.1[b]	576±2280[b]
				7,606±3,134m[c]		6.4±2.6[c]	1847±314[c]
Delayed dispersers	88	151	1,259±95 m	2,243±4,923m[b]	1.2±0.1	1.9±4.2[b]	161±774[b]
				2,804±2,538m[c]		2.4±2.1[c]	251±206[c]
Managed habitat	87	283	3,391±8,88 m	6,911±6,976m[b]	2.8±0.7	5.8±5.9[b]	1525±1553[b]
				12,642±3,020m[c]		10.7±2.6[c]	5102±291[c]
Unmanaged habitat	28	91	2,064±505 m	2,158±3,551m[b]	1.9±0.4	1.8.±3.0[b]	149±402[b]
				1,688±2,159m[c]		1.4±1.8[c]	91±150[c]
All dispersers	115	374	3,068±6,84 m	3,250±6,923m[b]	2.6±0.6	2.7±5.8[b]	337±1530[b]
				4,883±3175m[c]		4.1±2.7[c]	761±322[c]

[a] Assuming straight-line dispersal. The values for individuals dispersed outside the study site was based on the mean territory size within the study site

[b] Dispersal estimates and standard errors based on kinship coefficient (Rousset's distance) (Rousset 2000)

[c] Dispersal estimates and standard errors based on genetic distance (Loiselle et al. 1995)

To get an estimate of the effective population density (N_e), we used an approximation $N_e \approx N_{avg}/(V_m+V_f+4)$, where N_{avg} is the average number of breeders in the population, and V_m and V_f are the variances in number of offspring produced by males and females, respectively (Conner and Hartl 2004). To limit the possible effects of varying numbers of breeders and offspring, we estimated N_e on data for the years 2000–2004. Effective population density (D_e) was calculated by division of N_e with the total study area (excluding unsuitable habitat patches; 33.8 km^2).

Results

Direct assessment of natal dispersal distance

We re-observed 27 early dispersers (all ringed as nestlings) after dispersal either with the help of radio-tags ($N=12$) or through visual mark–recapture within ($N=12$) or outside our study sites ($N=3$; Table 3; Fig. 3). The two methods resulted in similar dispersal distance estimates and, on average, early dispersers moved 8,962±2,627 m (mean±SE), passing through 7.0±2.2 territories, assuming a straight dispersal route. The three untagged early dispersers that were located outside the study site had dispersed furthest (31,433± 20,562 m; Table 3; Fig. 3). We could confirm that 19 of the 27 early dispersers had become established members in the group to which they had initially relocated.

In contrast, offspring that delayed dispersal moved on average 1,259±95 m, passing through 1.2±0.1 territories, which is significantly less far than the early dispersers (Table 3; Fig. 3). There were a total of 179 delayed dispersers in our population during the study period. The eventual fate was known for 107 of these, of which 9 individuals became breeders on their natal territory (after both parents had disappeared), 79 individuals had dispersed to settle mostly in the neighbouring territory (maximum 4 territories away; Table 3), whereas the remaining 19 were retrieved dead within the borders of the natal territory (all killed by predators). Prior to dispersal, delayed dispersers have been observed to prospect at a maximum distance of 3 territories away from the natal territory. It is likely, therefore, that most of the delayed dispersers that were not re-observed after disappearing from their natal territory did not disperse outside the study site but were killed by predators (Griesser et al. 2006).

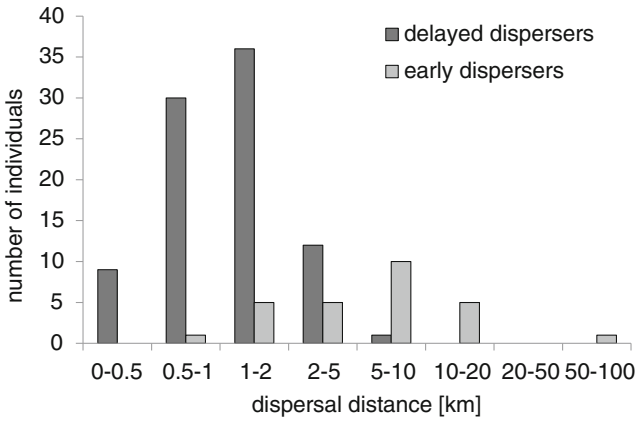

Fig. 3 Distribution of dispersal distances (in km) of all early dispersers ($N=27$) and delayed dispersers ($N=88$) displayed in eight distance classes. Early dispersers had significantly longer dispersal distances than delayed dispersers

Dispersal distances were best fitted with a lognormal distribution for all dispersers, early and delayed dispersers based on the AICC criterion (Table 4). However, when looking at the Pearson statistics (which assess the residuals of the errors of the fitted model), dispersal distances of all dispersers were best fitted by an exponential distribution, while those of delayed dispersers were best fitted by a normal distribution. Generalised linear mixed model analyses confirmed that early dispersers moved further than delayed dispersers (Table 5). Moreover, habitat structure affected dispersal distance: in the managed study site birds dispersed longer distances compared to those in the unmanaged area (Table 5). However, in both cases where the AICC and Pearson statistics did not correspond, the AICC-based models found significances, which were not found when using the error distribution with the best Pearson value (Tables 4 and 5).

The dispersal rate of early dispersers varied substantially between years (mean±SE, 0.58±0.05; min–max, 0–0.82 per territory; Table 2); however, since we were not able to distinguish between dispersal and mortality, this rate is likely to be too high. Similarly, the immigration rate of early dispersers that settled in the study site varied between years (mean±SE, 0.41±0.04; min–max, 0–0.81 per territory; Table 2). The dispersal rate and immigration rate were positively correlated (Pearson correlation: $R=0.55$, $p=0.02$), meaning that in years with a high proportion of dispersing fledglings (i.e. emigrating early dispersers), more early dispersers immigrated in the study population.

Indirect assessment of natal dispersal distance

A total of 24 loci were included in this study, and the number of alleles per locus ranged between 4 and 20, with expected heterozygosity ranging between 0.49 and 0.93 (Supplement Table 1). The studied population was found to be in Hardy–Weinberg equilibrium (Fisher's method for all loci, df=48, $\chi^2=\infty$, $p<0.0001$). Microchecker software indicated a heterozygote deficit for a few allele classes in locus SJ016, and it was excluded from further analysis.

On average, 69.2 breeders were present in the population each year between 2000 and 2004. The variance in the number of offspring was 1.22 for females (V_f), and 1.14 for males (V_m). Thus, we estimated the effective population size [$N_e \approx 8N_{avg}/(V_m+V_f+4)$; see "Methods") to be 85.85 individuals,

Table 4 Dispersal kernel functions fitting dispersal distances of all dispersers, early dispersers and delayed dispersers; fit assessed with help of the corrected Akaike Information Criterion (AICC) and the Pearson statistics

Distribution	All data		Early dispersers		Delayed dispersers	
	AICC	Pearson	AICC	Pearson	AICC	Pearson
Lognormal	*215.27*	0.40	*85.74*	*0.97*	*106.08*	0.18
Gamma	354.35	0.60	177.79	0.46	149.56	0.24
Exponential	392.52	*0.75*	176.53	0.66	219.04	0.45
T-distribution	463.90	16.27	190.09	64.26	210.81	0.26
Normal	766.20	41.80	224.77	167.89	234.30	*0.71*

Best values (lowest AICC, Pearson statistics closest to 1) are highlighted in italics; relying on AICC criterion to choose the best fitting distribution can lead to misleading results in particular if the data are underdispersed (see "Discussion")

and the effective population density (D_e) was estimated to be 2.54 individuals/km^2.

For all birds, there was a significant negative correlation between kinship and log geographic distance, but a non-significant correlation between genetic distance and log geographic distance (regression slopes denoted $blog_k$ and $blog_a$ respectively; $blog_k$=−0.0029, p<0.001; $blog_a$=0.0013, p=0.46; p values estimated by bootstrapping; Fig. 4). This pattern suggests a spatial autocorrelation with respect to kinship (i.e. isolation-by-distance), indicating that most dispersal is local (Beck et al. 2008). When the correlation between kinship and geographic distance was analysed only looking at delayed dispersers, the general patterns were the same, but the slopes were steeper ($blog_k$=−0.0060, p<0.001; $blog_a$=0.0040, p=0.09; estimated by bootstrapping). In contrast, the slopes were flatter when looking at this correlation for early dispersers only ($blog_k$=-0.002, p<0.0025; $blog_a$=0.0005, p=0.83; estimated by bootstrapping).

We calculated the dispersal distance for dispersers using both the kinship coefficient (Rousset 2000) and genetic distance (Loiselle et al. 1995) (details given in Table 3). Our analyses revealed that dispersal distance estimates for all

Table 5 Linear mixed model analysed of the dispersal distance using the distribution with the best fit based on AICC (for all lognormal distribution) and the distribution with the best fit according to the Pearson statistics; see Table 4

Effect	Estimate	SE	F value	p value
All dispersers (lognormal)				
Intercept	1.63	0.21	81.30	<0.0001
Dispersal timing	−1.14 (delayed disp<early disp)	0.18	39.54	<0.0001
Study site area	0.43 (unmanaged<managed)	0.14	8.56	0.0045
Method	−0.60 (V M-R<radio tag)	0.25	5.80	0.02
(exponential)				
Intercept	1.77	0.33	40.57	<0.0001
Dispersal timing	−1.98 (delayed disp<early disp)	0.28	50.23	<0.0001
Study site area	0.49 (unmanaged<managed)	0.21	5.28	0.02
Method	0.04 (V M-R<radio tag)	0.39	0.01	0.92
Early dispersers (lognormal)				
Intercept	1.45	0.45	53.18	<0.0001
Study site area	0.63 (unmanaged<managed)	0.42	2.25	0.15
Method	−0.53 (V M-R<radio tag)	0.40	1.78	0.20
Delayed dispersers (lognormal)				
Intercept	−0.06	0.11	3.21	0.08
Study site area	0.36 (unmanaged<managed)	0.12	8.33	0.005
(normal)				
Intercept	0.94	0.21	91.13	<0.0001
Study site area	0.41 (unmanaged<managed)	0.23	3.11	0.08

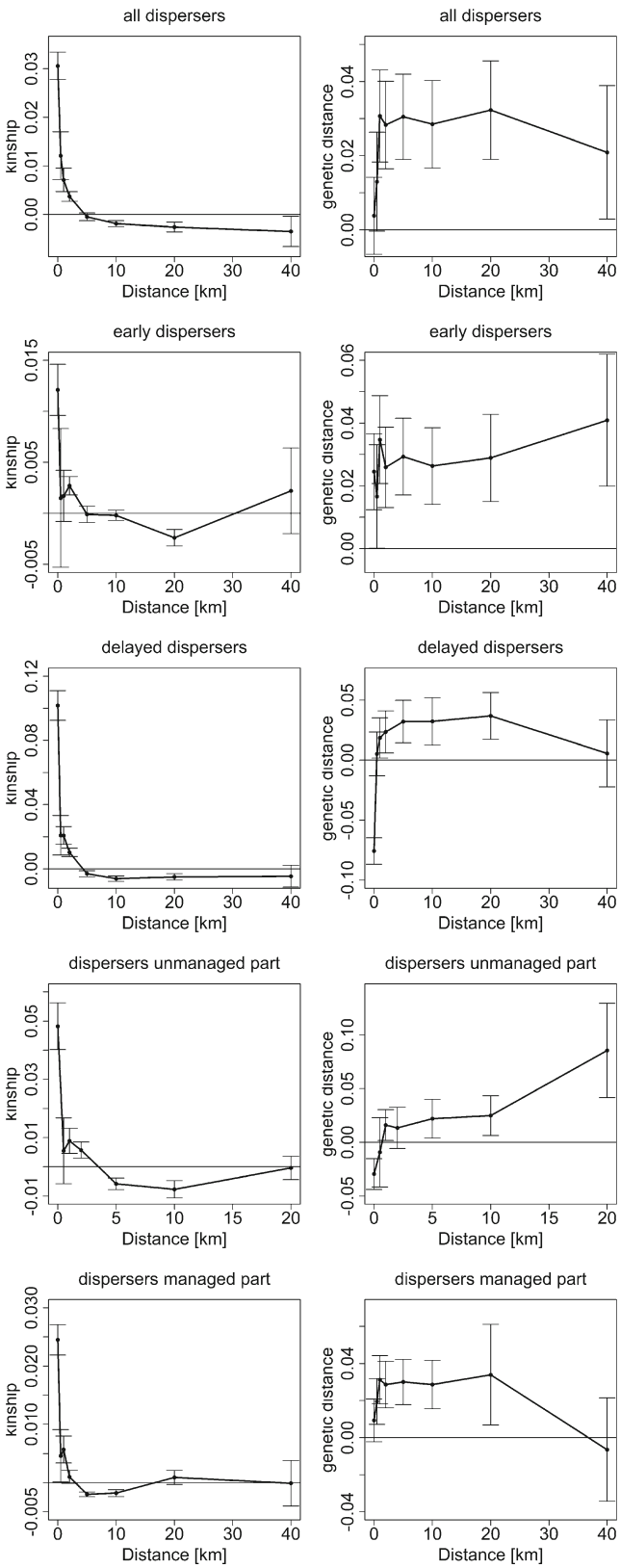

Fig. 4 Average kinship coefficient (*left hand graphs*) and genetic distance (*right hand graphs*) for all individuals, delayed dispersers, early dispersers, as well as all dispersers in the managed and unmanaged area of the study site. Mean geographic distance for 8 distance classes (in km). *Error bars* indicate the 95 % confidence interval obtained by 10,000 permutations of spatial group locations among spatial groups

dispersers, early and delayed dispersers as well as all dispersers in the managed and unmanaged habitat, closely matched observed dispersal distances based on direct methods (Table 3). Interestingly, for early dispersers, indirect estimates resulted in a shorter dispersal distance than both direct estimates, and a similar discrepancy was found when only looking at dispersal distances in the unmanaged habitat. However, over all dispersers the estimates based on the kinship coefficient and direct estimates almost matched.

The effective number of migrants moving between the managed and unmanaged areas of the study site was higher for delayed dispersers (13 migrants per year) than for early dispersers (7.3 migrants per year; Table 6). The Wright estimate (Wright 1931, 1943) showed the same pattern, where delayed dispersers had an infinite migration rate and early dispersers had 116 effective migrants between the two areas. Using direct methods, however, we only observed two early dispersers moving between the managed and unmanaged area of the study site during the study period where we ringed nestlings in both areas (total number of ringed early dispersers, 339 in 7 years; Table 2 and Fig. 2).

Discussion

Direct and indirect (genetic) dispersal estimates

In Siberian jays, the dispersal distances estimated from two direct measures (radio-tag, visual mark–recapture) corresponded closely to the dispersal distances obtained from indirect measures (micro-satellite data). For early dispersers where we had data for all three methods, the two direct methods resulted in almost identical estimates, while both indirect methods underestimated dispersal distance by 53 % (when using kinship) (Rousset 2000) or by 15 % (when using genetic distance) (Loiselle et al. 1995). In contrast, for delayed dispersers where we only had visual mark–recapture data, the direct method resulted in a longer dispersal distance than the indirect methods (78 % respectively 122 % more). These contrasting patterns are most likely to be reflecting the fact that delayed dispersers have higher lifetime reproductive success than early dispersers (Ekman et al. 1999).

A big difference between the three methods is the price and time needed to sample one disperser. Molecular estimates are 22–130 times cheaper and 31–67 times faster (depending on whether samples have to be collected in the field or already exist; Table 1). A surprising result is that in our study system assessing dispersal with radio-tags is cheaper and faster than through visual mark–recapture.

Table 6 Multilocus estimates of the effective number of migrants (*Nm*) according to (Slatkin 1985) between the managed and unmanaged area of the study site all dispersers, delayed dispersers and early dispersers

Managed vs unmanaged	$N=10$[1]	$N=25$[a]	$N=50$[a]	Migrants after size correction[a]	$N_e m_e$ [b]
all dispersers	177.5	43.0	23.7	6.5	58.3
delayed dispersers	273.2	62.0	33.4	13.0	∞[c]
early dispersers	106.4	27.8	15.7	7.3	115.8

[a] Three estimates of *Nm* are provided, where *n* is number of individuals sampled in each deme and the corrected estimate is adjusted for our sample size provided using the values from the closest regression line published by Barton and Slatkin (1986)

[b] $N_e m_e$ was calculated according to Wright (1931, 1943, 1951)

[c] Negative c_{st}, adjusted to 0, gives infinity

The key finding that early dispersers moved further than delayed dispersers confirmed the results of earlier studies in this system (Ekman et al. 2001, 2002; Griesser et al. 2008), and we discuss the reason behind this difference below. Moreover, our analyses showed that dispersal distances differ between the two study site areas. In the managed area, dispersal distances were about 60 % longer than in the unmanaged area of the study site (3,391 m vs. 2,064 m; direct estimates; Table 3). This difference in dispersal distance is confirmed by indirect estimates, that in the managed area estimated 104–273 % longer dispersal distance than direct estimates, but in the unmanaged study site, the indirect estimates matched (kinship coefficient, 5 %) or slightly underestimated dispersal distance (genetic distance, 18 %) compared to direct estimates. Thus, in our system, dispersal is influenced by habitat quality, where dispersers in low quality habitat disperse further than those in high quality habitat, confirming findings from other studies (Coulon et al. 2010). Given that habitat quality (i.e. gap size) has been found to affect dispersal movements even at small scales (Coulon et al. 2012), habitat quality gradients can influence the accuracy of genetic dispersal distance estimates.

How accurate are our dispersal estimates?

Observing long-distance dispersal requires a large number of radio-tagged birds and the ability to track the birds after dispersal. Since we were able to recover all of the radio-tagged dispersers that were followed after leaving the natal territory, the dispersal distances reported here are not biased towards short-distance dispersers. Moreover, for early dispersers all three methods resulted in similar dispersal distances, suggesting that these estimates are robust. This confirms findings of earlier studies assessing the reliability of different dispersal methods (Koenig et al. 1996), and recent development of new methods may allow the bias in dispersal distance to be assessed (Hirsch et al. 2012). However, our analyses demonstrate that using an information criterion approach (AIC) to fit the best matching dispersal kernel function might result in misleading results, since the AIC criterion benefits from underdispersed data, resulting in an "overfitted" model (S.M. Drobniak, personal communication). Instead, we advise using a method that analyses the variance structure of the fitted model, such as the Pearson statistics.

The use of radio-tags for tracking dispersers is still limited due to cost, labour and the weight of radio-tags. Technological advances will hopefully overcome the lack of a cheap method that allows us to describe accurately the distribution of dispersal distances in species with small body size soon (Kissling et al. 2013). Nevertheless, distance tracking does not provide us with all the answers regarding the factors that affect the evolution of dispersal (see below) (Doerr and Doerr 2005; Roshier et al. 2008), but alternative methods such as encounternet technology (Rutz et al. 2012) can provide information on social interaction between individuals in the absence of direct observation.

Our study is among the first to compare dispersal estimates using the three main methodologies (visual mark–recapture, radio-tagging, molecular assessment). Other studies comparing direct and indirect molecular assessment of dispersal distances also found that the two estimates were similar (Sumner et al. 2001; Vandewoestijne and Baguette 2004; Aspi et al. 2006; Watts et al. 2007; Coulon et al. 2008), but contrasting results can arise due to a number of factors: Indirect methods reflect both past and present dispersal events and rely on the interpretation of genetic data, which may be inaccurate in particular when a low number of molecular markers with a low level of polymorphism are used (Bossart and Prowell 1998). Accordingly, a high number of microsatellite loci increases the accuracy of estimating dispersal distance (Broquet and Petit 2009), and the number used here (23 loci, 11 loci with more than 10 alleles) is enough for accurate estimates of dispersal distances. Discrepancy in results from using direct and indirect methods of measuring dispersal may also stem from the fact that indirect methods only reveal effective dispersal but fail to detect unsuccessful dispersers (Table 1; Fig. 1) (Broquet and Petit 2009). In contrast, dispersal events recorded with direct methods do require the downstream breeding success of the disperser to

be followed. Thus, it is important to keep in mind that dispersal per se does not result in gene flow, i.e. a signal that is detectable with indirect methods. Finally, our results also show that habitat quality gradients can create differences between direct and indirect dispersal estimates, where the indirect method results in more extreme values compared to the overall mean dispersal distance.

Groups of individuals from the same population have been analysed to study sex-biased dispersal and differing patterns of genetic population structure in males and females (Hazlitt et al. 2004; Double et al. 2005), but not to study differences in dispersal timing between individuals, as is the case in this study. However, finding a difference in dispersal distance in relation to timing reveals neither the mechanism involved, nor the consequences thereof, which is important to understand the evolution of dispersal strategies.

Why do early and delayed dispersers differ in their natal dispersal distance?

In Siberian jays, natal dispersal decisions are affected by a variety of social interactions at different stages of dispersal. Early dispersers are constrained in their movement and settlement decisions by delayed dispersers and early dispersers that have already settled and chase them off their territory (Griesser et al. 2008). Thus, early dispersers mainly settle in territories without delayed dispersers of the same age (Griesser et al. 2008), and social interactions make the effective dispersal path much longer than the straight line distance between natal territory and settlement (Griesser et al. 2008). This discrepancy is only apparent when following dispersers closely during the dispersal phase (Doerr and Doerr 2006; Griesser et al. 2008). Since early dispersers only settle in existing groups (Griesser et al. 2008), suitable habitat patches may remain empty after local extinction (Griesser et al. 2007). Thus, the population dynamic in this species is strongly affected by the social interaction between resident individuals and dispersers (Nystrand et al. 2010).

Social interactions are also the reason why delayed dispersers have very short natal dispersal distances. These individuals gain direct fitness benefits from associating with their parents beyond independence (Griesser 2003; Griesser and Ekman 2004, 2005), boosting their survival (Griesser et al. 2006; Griesser 2013) and securing access to high quality breeding openings (Ekman et al. 1999, 2001; Nystrand et al. 2010). A similar correlation between dispersal distance and fitness proxies was found in Florida scrub jays (*Aphelocoma coerulescens*), where long distance dispersers were less successful breeders than short-distance dispersers (Coulon et al. 2010). However, in another group-living bird species (Pied babblers, *Turdoides bicolor*) kinship had the opposite effect on dispersal distance, which was suggested to be a result of inbreeding avoidance (Nelson-Flower et al. 2012).

What do direct and indirect, genetic estimates not tell us about dispersal?

The key strengths of genetic dispersal assessment have been mentioned above (*a posteriori* identification of dispersers, low cost, detection of long-distance dispersal events, assessment of population structure). Nevertheless, most studies assess only the dispersal distance or rate, which does not reveal which factors are responsible for dispersal decisions and how these are affected by conspecifics and therefore do not give a comprehensive understanding of the evolution of dispersal strategies. It is important to keep in mind that the three key methods used to assess dispersal all differ in what they can reveal about dispersal (Table 1; Figs. 1 and 2).

The direct assessment of dispersal using radio-tags is time consuming and costly but can give insights into the proximate behavioural and social mechanisms of dispersal during the departure, movement and settlement phase (Table 1). For example, an intensive study of the dispersal pattern of two sympatric Australian treecreeper species revealed differences in the search strategies of juveniles: The cooperatively breeding species dispersed much shorter distances than the pair breeding species that also used more surreptitious search strategies (Doerr and Doerr 2005, 2006). Using satellite telemetry or geolocators instead of field assessment of dispersal with radio-tags can reveal more large-scale movement patterns. An illustrative example is a study that looked at the movement patterns of the Grey Teal (*Anas gracilis*) (Roshier et al. 2008). In this species, dispersal movements between wetlands vary across geographic scales and between individuals. Similarly, results from studies using geolocators showed differences in migratory movements both within and between species (Stutchbury et al. 2009; Catry et al. 2011), highlighting the importance of assessment of dispersal at the individual level with direct methods.

Knowledge of how species move through space and which factors affect their search path is a fundamental component of dispersal (Zollner and Lima 1999). Nevertheless, the discrepancy between models and field data regarding movement patterns point to the fact that more data from field studies are needed. A model looking at dispersal strategies predicted that straight or nearly straight search movements would be optimal (Zollner and Lima 1999), while data of field studies show that dispersal often resembles a random walk (Doerr and Doerr 2005; Griesser et al. 2008; Roshier et al. 2008).

Conclusions

Our findings support the idea that direct and molecular methods of dispersal distance can result in similar results, even when applied to a system with different dispersal timing between individuals, and differences in habitat structure

affecting dispersal distance (Coulon et al. 2012). Direct and indirect methods, however, differ in what they can tell us about dispersal, and it is therefore advantageous to combine these methods (Peacock and Ray 2001; Alcaide et al. 2009; Rollins et al. 2012). In particular, the value of direct observations seems to be less and less appreciated, yet this method allows detailed insight into the proximate mechanisms affecting dispersal decisions and improves indirect assessment methods. By combining genetic data and direct social network analyses, it is possible to improve estimates of dispersal rate of individuals immigrating from outside the study population (Rollins et al. 2012). More importantly, studies in Siberian jays and other model species highlight that a good understanding of the evolution of dispersal strategies requires insight into all phases of dispersal. It is therefore recommended to conduct in-depth studies in well-studied model species (Clutton-Brock and Sheldon 2010) that would allow us to understand the influence of resident individuals and social interactions on dispersal decisions and the long-term fitness consequences thereof (Coulon et al. 2010).

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